

6. A View of Species

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My predilection in biology is to search for an effective evolutionary synthesis and a credible biological world view. Though not consciously a structuralist, I appear to share aspirations and goals with at least some structuralists. For example, I feel empathy with the structuralists' concern for wholeness, the ideas of transformation and self-regulation, if I have conceived these abstract ideas in Piaget's way.

Evolution, particularly species theory, is a significant subject because it illuminates much of what we see in the living world and our own species. Such illumination can have far-reaching consequences not only in population biology, but for the way we see ourselves, as became obvious when society first realised that the human state was not the ultimate creation of a deity but the product of a process which had yielded millions of other such products, each remarkable in some way. This was a revolution in human thought appreciated by rather few other than philosophers. The pursuit of such an intellectual path is only possible for members of *Homo sapiens*, a fact which helps identify a more particular evolutionary perplexity: the achievement by humans of the conceptual powers which enable such a problem to be recognised.

In this chapter I shall consider from perspectives which may interest structuralists a number of evolutionary topics related to natural diversity, species and the origin of species. Although I retain common ground with the movement which led to the so-called 'modern synthesis' of evolutionary thought, I do not subscribe to a number of ideas and viewpoints which currently receive general support. My aim is to present a heterodox ordering of well-known information in order to provide a new perspective, rather than new facts. In particular, I wish to emphasise the fundamental importance of genetical species in evolution, despite their origins as serendipitous consequences of sex. I shall also draw attention to the evidence indicating that many of the transcending steps in the long story of life on earth have occurred by processes not encompassed by the 'modern synthesis'.

A VIEW OF SPECIES

'Man has always been fascinated by the great diversity of organisms which live

in the world around him. Many attempts have been made to understand the meaning of this diversity and the causes that bring it about. To many minds this problem possesses an irresistible aesthetic appeal' (Dobzhansky, 1951).

In 1952 I first read these words and became fully conscious of this irresistible appeal to the mind. This early interest in eukaryotic diversity, in turn, led to my interest in the genetic nature of species because species are the units of diversity. To address the problem of diversity from the basis of species it is evidently necessary to understand, at least in broad genetic terms, how new species might arise. Darwin failed to provide any answer which satisfies us today to the principal problem he addressed: the origin of species. It is now apparent that this is because he did not have, and, indeed could not have had at that time, a clear picture of the genetic nature of species. Therefore, he was unable to address the subject of his book in an adequate way. In fact, he conceived species morphologically, though through evolutionary eyes, and set out to answer his big question from this viewpoint. Now, however, we can see that an understanding of species diversity depends on a basic understanding of the genetics of speciation, which, in turn, is constrained by our view of species.

After some twenty years of rather unquestioning support for the prevailing Biological Species Concept (or, Isolation Concept), during which I applied it to the study of problem species in Diptera of medical importance (e.g. Paterson 1956, 1962, 1963, 1964a, 1964b, 1964c, 1970), the shortcomings of defining species in terms of their reproductive isolation from other species began to become manifest. The process of disillusionment was accelerated by my reading of George Williams' (1966) book *Adaptation and Natural Selection*, which upset my understanding of natural selection and which has continued to influence me to this day. In this work Williams set out to instil some discipline and rigour into evolutionary discussions involving adaptation through natural selection. Structuralists would probably wish to avoid this approach altogether, and I sympathise with this attitude to the extent of being interested in exploring the possibility of reducing my reliance on explanations involving the concept of adaptation through the differential transmission of alternative alleles.

In searching for a more satisfactory approach to species than in terms of reproductive isolation mediated by isolating mechanisms, I went back to first principles, in this case, sex, and asked the question: how, in general terms, is the inherently improbable process of fertilisation in biparental eukaryotes achieved?

A little exploration and a little thought revealed that every biparental organism must possess a set of characteristics which are effective in bringing about fertilisation under the conditions prevailing in the organism's normal environment. This is really axiomatic and applies to all biparental eukaryotic unicells, to fungi, plants and animals including *Homo sapiens*. The characteristics of these *fertilisation systems* vary with the ways-of-life of the organisms and with their normal environments, but in all cases known to me

they are clearly necessary for the fundamental process of fertilisation to occur. In George Williams' terms, the function of the fertilisation system is the achievement of fertilisation under normal natural conditions, no more and no less. The fertilisation system as a whole can thus be regarded as a complex adaptation.

Before proceeding with this argument I should deal with a potent, all-pervading source of confusion. Darwin viewed species in morphological terms though he did this in quite a sophisticated way, using evolutionary explanations (Darwin, 1859: 423-4). He saw the 'fitness' of an organism in terms of its aptness for life in its normal environment. Accordingly, he saw the rather extreme secondary sexual characters of some species, particularly birds such as the peafowl, as leading to reduced fitness in his sense of the term. A peacock's train can hardly fit it for life in its normal wooded environment, and might well reduce its chances of surviving predation. To accommodate such situations Darwin introduced the concept of *sexual selection*. Instead of simply noticing that every biparental eukaryotic organism is necessarily equipped with a system which leads effectively to fertilisation, he believed that a further set of characteristics often evolved under the different selection pressure arising from either male/male competition for females, or, in some cases, inter-female competition for males. Whether sexual selection in the strict sense really is a significant factor in evolution is still far from certain, despite the burgeoning literature which assumes it is (Halliday, 1983). In any case, it is seldom noticed that if it does exist it is an additional system (complex adaptation) to the fertilisation system, and that it has evolved under distinct selection pressures and had a distinct function. Thus, looking at reproductive systems of organisms like peafowl or birds-of-paradise, one needs to be very cautious in disentangling the fertilisation system characters from possible characters evolved in response to competition for mates. In studying particular species I believe that one needs always to ask: can the reproductive behaviour of members of this species be entirely accounted for in terms of the fertilisation system alone? If the answer is yes, it is clearly unjustified to believe that they evolved in response to competition for mates. A great clarification of the literature on reproductive behaviour would immediately result if this distinction were to be made consistently.

I return now to my main theme to consider a major consequence of any fertilisation system appropriate to the organism's normal environment and way-of-life. The consequence is that such a specific fertilisation system effectively constrains the exchange of genes so that exchange effectively occurs within the group which shares the same fertilisation system, the same normal habitat and the same way-of-life. Obviously, such properties are the same as those characterising any genetical species.

To sum up these points, one can define a species in genetical terms as that most inclusive population of individual biparental eukaryotic organisms which share a common fertilisation system. Every fertilisation system defines locally

the field of gene recombination of a species. It is, perhaps, prudent to discuss this proposition briefly in order to provide a clear perspective. Fertilisation systems can differ markedly or only to a minor degree with the consequence that there is a continuum in difference between populations. At one extreme, two populations can comprise organisms with virtually identical fertilisation systems. At the other, we find organisms with fertilisation systems which are wholly different from each other, as between an ostrich and a ruby-throated hummingbird. Often, as in ducks (Lorentz, 1941) or Pelicaniformes (van Tets, 1965), components of the fertilisation system may be shared by different species with no loss of effectiveness.

Since my interest is in the understanding of the diversity in nature, I shall not be concerned with man-made situations. Lions and tigers do hybridize in zoos when confined to the same cage. However, the fertilisation system is here destabilised because it was not evolved to be effective in a zoo cage where no appropriate mates are present. Among plants a similar situation prevails in a botanical gardens where many species of related plants are artificially brought together. Another botanical example results from the destabilisation of fertilisation system through the disturbance of the environment (through human or natural causes) to such a degree that populations normally found in distinct environments are brought into proximity (Anderson's 1948 'hybridisation of the habitat').

A fertilisation system, I have already emphasised, is appropriate for the environment in which the organism normally lives and for its way-of-life (whether it is sessile or motile, diurnal or nocturnal, etc.). Under these circumstances the system is very stable. The individual characters are evidently subject to stabilising selection: aberrant individuals with inappropriate components to the fertilisation system will be less likely to fertilise or be fertilised. In motile animals, particularly, an important part of the fertilisation system is the specific-mate recognition system (SMRS) which serves to bring together potential mating partners. The SMRS characters are involved in the sending or receiving and processing of signals between mating partners or their cells (e.g. sperm and ovum, pollen and stigma). Sessile organisms, such as angiosperms or sessile molluscs, are much less dependent on the SMRS. Sessile organisms rely, inevitably, on vectors to transport their sex cells. These vectors are wind, water and animals (insects, birds and mammals). The signals between angiosperms and insects are not part of the SMRS, but are accommodations to a vector. Coadaptation between, say, a male signal and female receiver places a strong constraint on independent change in either the male or female component. The same is true for signals between a pollen grain and the stigma of the mating partner. SMRS signals, like the rest of the fertilisation system, are also usually apt for the organisms normal environment. Thus fireflies, moths and owls signal appropriately for nocturnal conditions. Forest birds and frogs are characterised by calls appropriate for transmission through dense vegetation (Morton, 1975). Birds of open

grassland signal visually as well as by sound, as sound is readily disturbed by wind (Morton, 1975), etc.

Large population sizes of species make it nearly impossible to change a coadapted signal from one stabilised (coadapted) condition to another for the whole population. For this and other reasons, speciation is believed to involve small populations (see below), and the termination of speciation coincides with the growth of the daughter population following the switch from directional to stabilising selection.

Thus, for three independent reasons, fertilisation systems are stabilised: their relationship to the population's normal habitat, the coadaptation of signals and receivers (and other aspects of their fertilisation systems and biologies), and the stability of large populations.

SPECIATION

From this view of species, one can understand a little of what must occur during the formation of a new species. The difficult task to be accomplished entails the changing of critical characters, including the fertilisation system, from one stable state, appropriate to the parental environment, to a new stable state, appropriate to the new environment to which the daughter population has become restricted.

The stable state of a species in its normal habitat can be changed to a new one only if its stability is first disturbed. For example, a fertilisation system will be destabilised if a small population is displaced to a distinctly different environment in which the characters of the fertilisation system, etc., will not be fully effective. Stabilising selection on these characters will then be replaced by directional selection which will lead to the spreading of alternative alleles determining a new phenotype more effective under the new conditions. A small population will facilitate the fixation of the alleles determining a new stable state. This applies to other adaptive characters such as feeding and nesting habits, and predator avoiding behaviour as well. Achieving a new stable state involves the adjustment of all such characters of the organisms to a new stable state.

Since speciation entails small populations, the bottleneck probably facilitates the fortuitous fixation of certain alleles and chromosome arrangements at the same time. Of course, the genetic variation fuelling the selective process may involve pleiotropy.

Thus, the 'normal habitat' of a species is thought to approximate in key features to the one in which speciation occurred. Changing habitat is a major revolution for organisms, and available evidence convinces me that it corresponds with a speciation or subspeciation event.

In the normal habitat all environment-related characteristics of members of a species are under stabilising selection, not just the fertilisation system including the SMRS. Thus, for effective development to occur, fertilised eggs of fish, frogs, or mosquitoes, for example, must develop within certain limits.

The development of the eggs of the subarctic mosquito, *Aedes stimulans*, normally occurs at low temperatures. If the eggs are kept at higher temperatures, development is aberrant (Horsfall and Anderson, 1963). Similarly, organisms in their normal habitats are efficient in feeding, avoiding the predators with which they are in contact, and, in some cases, nidification. This efficiency is seriously disrupted if organisms are displaced into effectively different habitats. Judging by the prevalence of simplistic models for how habitat change might occur, it is not well appreciated that change of habitat for any group of organisms requires a major genetic revolution. Mayr (1963) and others have drawn attention to the fact that speciation entails many changes in ecological characteristics, but this has not always been understood.

The work of Coope and his colleagues (Coope, 1979 for review) on Quaternary fossil beetle assemblages in peat bogs in Europe and America has provided much telling support for these points. His demonstration of the stability of organism-habitat relationships despite the overwhelming environmental changes due to advancing or retreating ice is of fundamental importance in understanding why species are so stable and must be taken into account in formulating any views on the diversity of the living world. Coope has pointed out that speciation is not a common outcome of such catastrophic environmental events. For it to occur, organisms must be 'trapped' in front of a mountain range, for example, so that retreat ahead of the change by the organisms and their environment is blocked. Even then extinction is a more general outcome than is speciation or subspeciation.

Restriction of organisms to new environmental conditions as a necessary prelude to speciation can occur in many ways. Relic populations can commonly be observed today telling of former wider distributions under different climatic regimes. These provide us with illustrations of what Coope is saying. Increased aridity and cooling seem to be particularly effective in restricting organisms to new habitats through the progressive degrading of relic communities. Of course, islands at appropriate distances from continents provide other possible conditions which lead to speciation through destabilising the species which invade them adventitiously. Other possibilities exist as well.

OTHER PROPOSED MODES OF SPECIATION

Many other modes of speciation have been proposed (White, 1978; Mayr, 1963, 1987), but they have all been conceived with the constraints of the isolation concept in mind. It should therefore be noted that the model of speciation which I call allopatric speciation is genetically different from the well-known model of geographic or peripatric speciation long advocated by Ernst Mayr (1942, 1954).

Mayr's model and mine share common ground in requiring the physical isolation of small populations for sufficient time for speciation to occur, but differ because Mayr was obliged by his species concept to rely on pleiotropy to

modify the existing 'primary' isolating mechanism (usually some form of postmating isolating mechanism). He believed that other isolating mechanisms often evolved later under natural selection when daughter and parent populations again met (Mayr, 1963: 551). I have previously provided details of the difficulties existing for the various models generated by the isolation concept (Paterson, 1978, 1982a, 1985), and have argued that no *prima facie* evidence exists to show that any species has ever arisen by any model of speciation other than some form of allopatric speciation (Paterson, 1981, 1985, 1987), and that substantial difficulties confront models invoking selection for reproductive isolation (Paterson 1978, 1985).

It should be reiterated that models of speciation are logically derived from concepts of species so that when a concept of species is abandoned, all its dependent speciation models must be discarded with it.

CONSEQUENCES

Interesting genetic and ecological consequences flow from the picture of species in terms of specific-mate recognition, and how they are likely to arise. These consequences lead us to look at the data of nature with different eyes. The prevailing concept of species, the isolation concept of Dobzhansky and Mayr, defines one species in relation to other species, which leads to many problems which I have outlined before (Paterson, 1978, 1980, 1981, 1982a, 1985, 1987). Derived consequences from the isolation concept are quite different from those from the recognition concept, despite Mayr's (1987) assertion that the two concepts can be seen as 'the two sides of a single coin'. It is not possible to compare the consequences of the two concepts here, but some consequences of the recognition concept will be discussed.

Although natural selection is invoked as part of the process of speciation, it is merely part of the process of organisms adapting to new conditions. If speciation results from this it is fortuitous, and is an extreme of a continuum in degrees of divergence. In George Williams' terms species are not 'adaptive devices' but incidental consequences of adaptation ('effects'). This is a fundamentally important insight. Darwin reached a similar conclusion but with a limited understanding of species and speciation. To many this conclusion is unacceptable when applied to our own species (Paterson, 1982b, 1985, 1987). However, it has a far wider significance than this. For example it affects fundamentally our views on ecology and the causes of biological diversity (Paterson, 1985, 1986; Walter *et al.*, 1984; Hulley *et al.*, 1988).

The model of speciation which follows from the recognition concept also directs thinking in particular directions and has important implications. It very firmly invokes speciation in small populations, despite population genetical reservations on the subject. This is in keeping with empirical evidence from actual speciation events of the past, and it provides a better understanding of why 'punctuation' should be a feature of the fossil record (Eldredge, 1971; Eldredge and Gould, 1972). The recognition concept is also

important in understanding the assembly of ecosystems and communities, and in interpreting biogeographical data.

The three reasons for the stability of species provide insights for the understanding of a number of aspects of evolution. They provide a clear explanation of the 'equilibrium' phase of Eldredge and Gould's 'punctuated equilibrium' view of the fossil record. Species homeostasis has also an important bearing on the long and drawn out debate on sympatric speciation. Member organisms of a species in their normal habitats are subject to mainly stabilising selection. There is no pressure to speciate under such conditions because there is nothing to disturb the existing stable state. This view contrasts with the view of species as 'adaptive devices', which diverge in order to exploit more fully natural resources by occupying 'unoccupied niches'. Under the recognition concept this viewpoint is wholly unjustified. The niche occupied by the organisms of a species is not a property of the environment but is largely a reflection of their genotype (Paterson, 1973; Walter *et al.*, 1984). Once this is understood it is no longer a puzzle why species do not occupy 'niches' which appear to ecologists as so temptingly 'vacant'. Expectations are likely to remain unfulfilled if they stem from inappropriate analogies with human economic systems.

When species are understood to be extreme incidental consequences of adaptation to new environments, hybrids and hybridisation are seen in quite new ways. As J. L. Crosby (1970) once warned, the consequences of hybridisation may be good or bad and are decided by natural selection, not by our biases and idealistic preconceptions. Once the preservation of 'species integrity' or 'species purity' is seen to involve deep cultural preconceptions (Paterson, 1982b, 1985, 1987) we stop expecting hypothetical 'isolating mechanisms' to be 'reinforced' by selection, and expect natural selection simply to act to maintain viability. A full understanding of what is occurring in hybrid zones or in hybrid populations demands a proper understanding of the nature of species.

Species integrity is conventionally seen as being protected from destruction by so-called 'isolating mechanisms'. Few pause to wonder why these 'isolating mechanisms' are often protecting hybrid genomes as in the case of polyploid species of plants. These are widely accepted as generally being allopolyploids (Amphiploids). Are the isolating mechanisms in such cases still protecting 'species integrity'?

Some authors (Scoble, 1985; Templeton, 1987) criticise the recognition and isolation concepts for not covering uniparental organisms. Both Dobzhansky and I have accepted that this desire for generality has its roots in taxonomy (see Mayr's 1963: 28 approach), but reject it because our aim is to understand natural diversity, not to classify organisms. Most eukaryotes are biparental, or are at least facultatively biparental, and so are to be understood in terms of a genetical concept. A few primary uniparental eukaryotic organisms may exist (amoebae, euglenoids) but most are derived from biparental organisms.

Widening a species concept in order to cover these secondarily uniparental organisms destroys the explanatory power of a genetical concept, and involves the conflation of concepts of species from two quite distinct fields of scientific endeavour (Taxonomy and Evolutionary genetics) (Paterson, 1981). Rather than attempting to devise a concept that brings 'chalk and cheese' under one heading, I prefer to account for the secondarily uniparental eukaryotes by trying to understand their origin. Understanding that they very generally bear signs of a hybrid origin, uniparental eukaryotes, e.g. allopolyploid plants, can often be recognised as examples of organisms which have 'escaped from hybridity' (Darlington, 1958; Grant, 1971; Paterson, 1981, 1985, 1987). This alternative viewpoint is in accordance with the idea that, as usual, natural selection acts on hybrids by selecting for viability (Paterson, 1978).

This brief catalogue is not comprehensive in listing the important new insights deriving from the adopting of the intuitively appealing and evidently effective recognition concept of species. Active application of the ideas will readily reveal many more.

DISCUSSION

'The thesis that new facts are always responsible for the ultimate clarification of scientific problems is becoming increasingly questionable' (Mayr, 1976: 331).

Mayr is here drawing attention to the fact that the way we look at problems in science is often more critical in clarifying them than is the provision of yet more empirical data.

Some evolutionists still feel happy with the 'evolutionary synthesis'. This is depressing to me and, I am sure, to many others, in the face of the remarkable empirical and theoretical advances of this period. In fact, I believe the advances made in the last forty years have revolutionised our evolutionary view of life, and what is new should be reflected in our synthesis. On the other hand, it would be surprising if nothing remained of the very impressive edifice erected in the thirties and forties. Perhaps reformatting our views on evolution should be our aim rather than debating whether a new synthesis is required or not.

To many the core of the evolutionary synthesis is the biological species concept. Certainly much in the synthesis is related to species theory. It follows, therefore, that a significant change in viewpoint on the genetic nature of species is likely to be an important reason to reformulate the evolutionary synthesis. As the outline provided above will have demonstrated, the Recognition Concept does constitute a new way of looking at species in genetic terms, and its adoption will thus ensure that any evolutionary synthesis built around it will be significantly new.

Besides, we must also incorporate the appreciation that so transcending a step as the evolution of the eukaryotic cell entailed a process not envisaged under the world view of the evolutionary synthesis: symbiosis. Today we

appreciate that symbiosis involves a radical form of genetic and systems recombination quite unimagined, or, at least, unconsidered in 1942. The evolutionary synthesis has never provided a satisfactory explanation of the evolution of sex. The cannibalism theory of the evolution of sex (Margulis and Sagan, 1986) provides a reasonable scenario of how sex might have evolved. This model cannot be considered part of the evolutionary synthesis despite it having been considered seriously by Maynard Smith in 1958. We might eventually achieve a more credible and general understanding of the evolution of sociality when we rethink it in comparable stochastic terms, and abandon the procrustian task of forcing the problem into a neo-Darwinist framework. The neutral theory of molecular evolution (King and Jukes, 1969; Kimura, 1969) has provided many insights which would not have been forthcoming in the light of the evolutionary synthesis, and I am sure there are more insights to come from it.

Although I have not exhausted the revolutionary ideas outside the evolutionary synthesis, enough examples of major consequence have been cited to illustrate the fact that we now have at our disposal the elements of a quite radically different view of evolution than was available in the thirties and forties. A synthesis of these elements has not yet been made, because, besides it being a formidable task for which few are fitted, I believe few have attempted to think through the consequences. Or perhaps those who have done so have drawn back in awe at the picture partially glimpsed.

Much of this modified world view will be acceptable to structuralists, but probably not all. At present I still retain a place for functionalist explanations, though I check their credentials individually. But I certainly do not exclude the explanatory explanations of physical scientists or structuralists (Rosenberg, 1985). I don't believe this stand constitutes fence-sitting, as that has not really been my style in the past; rather I think it is because both kinds of explanation can, at times, provide understanding. A hope we might cherish in support of Mayr's statement with which we began this discussion is that scientists will in future spend more time in considering theory instead of generating more and more empirical data in attempting to answer inappropriately posed questions.

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